

COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, XVII.

PRELIMINARY OBSERVATIONS ON THE PROBLEM OF TRANSITIONS FROM BROAD TO TERETE LEAVES¹

† I. W. BAILEY²

TWO OF THE MOST significant phenomena in adaptations of the Cactaceae for survival in arid environments are (1) the retention of moisture in abundantly occurring "mucilage" and (2) the reduction of leaves in Opuntioideae and their elimination in Cereoideae *with concomitant transfer of photosynthetic activity to green parts of stems*. Both phenomena merit more extensive and intensive investigation from morphological, ecological, physiological, and biochemical points of view than they have received thus far.

A morphologically and phylogenetically important aspect of the second phenomenon is the question, how many transitions from ancestral broad leaves to terete ones have developed in the Opuntioideae? In my extensive collections of *Pereskia*, *Pereskopsis*, and *Quiabentia* I have not encountered such transitions up to now. However, they do occur in certain representatives of the Opuntioideae, particularly in *Opuntia subulata* (Muehlenpf.) Engelm.

In my collection of this plant [*Moran 7268*] the leaves are relatively large and persistent. The vasculature in the shorter, broader, less frequently occurring ones closely resembles that which occurs in leaves of comparable forms and sizes of *Quiabentia pereziensis* Backbg. (compare Figs. 1 and 2). In both cases the venation of the appendages is palmate as in *Pereskopsis* and *Quiabentia*, rather than dominantly pinnate as in the large, thin leaves of such more primitive pereskias as *P. sacharosa* Griseb., *P. grandifolia* Haw., *P. bleo* DC., and related species. For discussions of variations in the venation of leaves and cotyledons and their phylogenetic significance, see 1960 and 1965.³

In *Opuntia subulata* (*Austrocylindropuntia subulata* (Muehlenpf.) Backbg.) none of the abundant more elongated leaves, although relatively slender, are truly terete, i.e., circular in cross section. All of them exhibit

† This paper was completed by Professor Bailey shortly before his death on May 16, 1967. He had planned the illustrations and discussed them with the artist, Elmer W. Smith, who completed them subsequently.

¹ *Terete* is defined in standard dictionaries as cylindrical and tapering with circular cross section.

² This investigation was supported in part by a grant from the National Science Foundation, GB-2935.

³ Previous papers of this series are listed by their dates of publication.

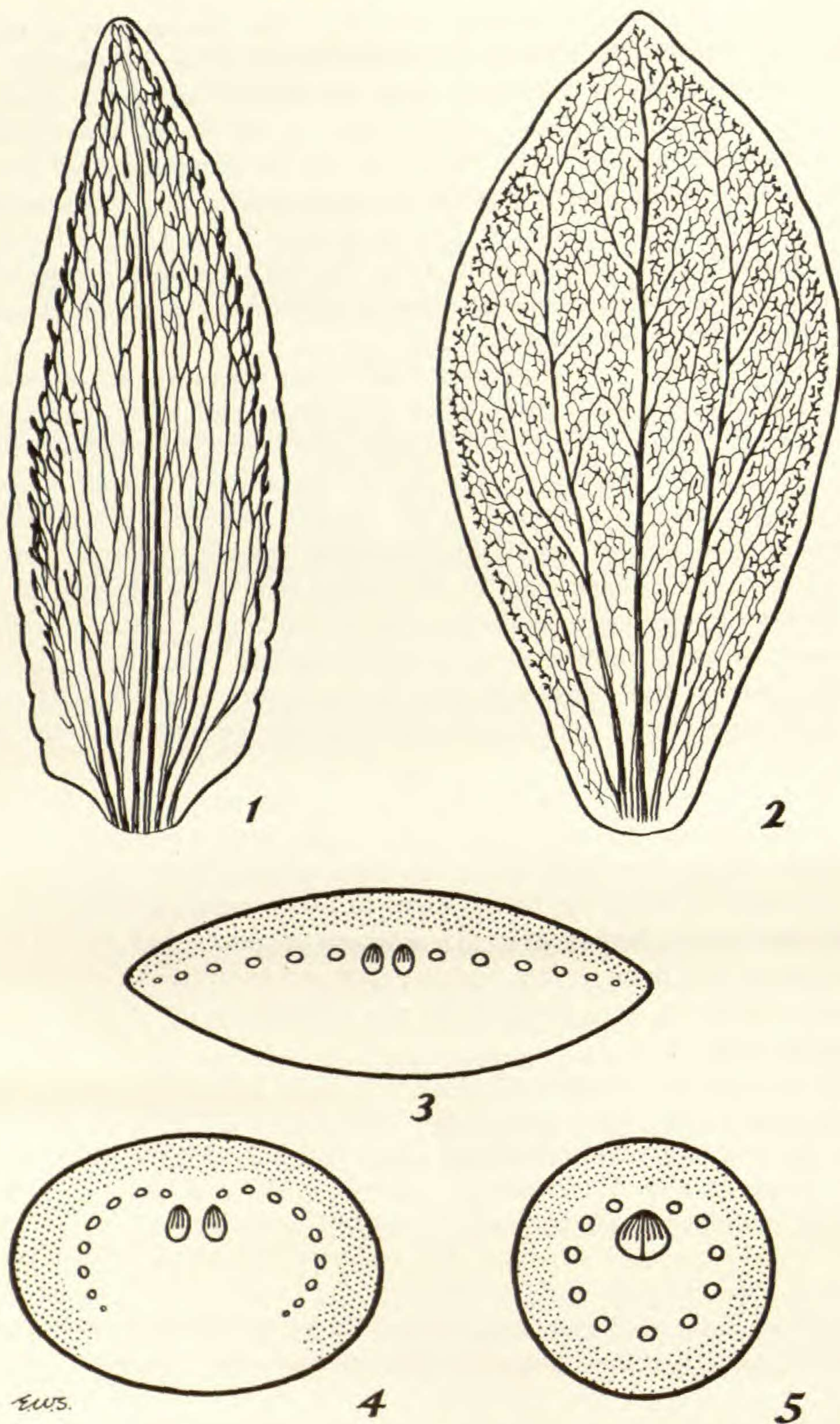
more or less extensive broadening laterally. The two systems of veinlets in opposite sides of the lamina are derived largely from independent vascular strands extending outwardly from the base of palmately veined appendages, except in the upper central parts of the leaves where more or less numerous veinlets may be related to the conspicuous paired vascular traces in the center of the lamina. In such leaves, the two systems of veinlets tend to curve more or less extensively in opposite sides of the lamina toward the abaxial surface (FIG. 4). As they do so, more or less characteristic palisade tissue becomes concomitantly extended laterally, but does not jacket the abaxial surface.

In contrast to this, the evanescent truly terete leaves of such opuntias as *Opuntia ficus-indica* (L.) Mill. and *O. cylindrica* (Lam.) DC., particularly during earlier stages of their development, are jacketed by palisade tissue (FIG. 5). In such tiny terete leaves, the vasculature is much modified. The paired traces in the center of the lamina commonly are massive in appearance and exhibit frequently occurring fusions. Independent vascular strands in the basal part of the lamina tend to be eliminated. The two systems of veinlets in opposite sides of the lamina, although reduced and modified, commonly tend to be conspicuously coarse and related to the two more or less fused mid-veins in the center of the lamina rather than to independently occurring lateral vascular strands as in the large leaves of *O. subulata*.

In my collections of *Opuntia ficus-indica* preserved in FAA the leaves vary from circular to oval and exhibit conspicuous adaxially oriented curvatures which may have been intensified during fixation and dehydration. In some of them the two systems of coarse veinlets coalesce in the abaxial side of the lamina (FIG. 5), whereas in others they fail to do so. According to Dr. Boke (1944, and personal communication) the two systems of veinlets in *O. cylindrica* do not coalesce in the abaxial side of matured leaves.

Thus, in dealing with transitions from broad palmately veined leaves to truly terete ones, there are three trends of phylogenetic specialization which merit detailed consideration. These are (1) changes in the occurrence, structure, and distribution of palisade tissue, (2) alterations in the principal vascular strands that extend outward from the base of palmately veined appendages, and (3) reduction and modification of two systems of veinlets in opposite sides of the lamina.

The large, thin, pinnately vascularized leaves of primitive pereskias do not form typical palisade tissue on their adaxial side. However, there is a more or less conspicuous tendency to do so on the adaxial side in the case of the palmately veined leaves of *Pereskia* and *Quiabentia* (FIG. 3). It is evident in the limited collections available to me that the second and third trends of morphological specializations in terete leaves are not consistently similar in minor details of structure, even in different leaves from the same plant. Therefore, it is essential to obtain and compare leaves from as many representatives of the Opuntioideae as possible in a com-



FIGS. 1-5. Vascularization of leaves of Cactaceae. 1. Leaf of *Opuntia subulata* (the shorter, broader type of leaf occurring in this species). 2. Leaf of *Quiabentia pereziensis*. 3. Diagrammatic cross section of a leaf similar to that in FIG. 1 or to a typical palmately veined leaf of *Pereskia* or *Quiabentia*. Palisade tissue on the adaxial side is indicated by stippling. 4. Diagrammatic cross section of one of the more abundant elongate leaves of *Opuntia subulata*.

prehensive search for additional transitional stages in the development of terete leaves. Such an extensive investigation is being undertaken by Professor Norman Boke and myself.

In comparing the form and vasculature of modified leaves, it is necessary to avoid utilizing the appendages that occur on the uppermost external surface of the invaginated tori of flowering shoots. Such modified leaves in the Pereskioideae and Opuntioideae frequently exhibit conspicuous broadening at their base and patterns of vasculature which simulate those that occur in the first-formed tepals on the inner surface of the invaginated tori. These foliar modifications obviously present an independent phylogenetic problem and one that merits detailed investigation in the future. Therefore, in searching for transitions from broad leaves to terete ones, I have focused attention upon the foliar appendages of vegetative shoots and have avoided those occurring on the uppermost invaginated part of flowering ones.

Although possible variations in the form and major details of vasculature in the leaves of additional representatives of the Opuntioideae merit investigation, there is, even in limited collections now available, cogent evidence of the derivation of terete leaves from broad, palmately veined ones. It should be emphasized in this connection, that without knowledge of significant transitional stages occurring in such opuntias as *Opuntia subulata*, it might be erroneously assumed *a priori* that the highly modified vasculature of terete leaves is developed by transitional modifications of broad pinnately veined appendages.

The only cactus that I know of, exclusive of the Opuntioideae, which forms truly terete leaves is the genus *Maihuenia*. Three collections of *M. poeppigii* (Otto) Weber, obtained from Chile by Hutchison in 1951, are under cultivation at the University of California Botanical Garden in Berkeley, California. These plants have grown well in the open, flowering and fruiting annually. In material kindly sent to me [*Hutchison 306*], the numerous short, slender branchlets in the upper part of a plant bear compact clusters of terete leaves terminally. In such branchlets there is a more copious production of "mucilage" than I have observed in any other cactus. Furthermore, there is a very precocious development of encasing periderm in parts of stems immediately subtending the cluster of terminal terete leaves. Photosynthetic activity appears to be largely confined to these long-persistent appendages. The terete leaves at maturity are jacketed on all sides by very conspicuous palisade tissue which contains much enlarged and elongated mucilage cells. As in terete leaves of opuntias, there is a similar tendency for fusion of the paired traces in the center of the lamina, and the two systems of coarse veinlets coalesce in the abaxial side of the appendages.

Palisade tissue extends laterally but does not cover abaxial surface. 5. Diagrammatic cross section of truly terete leaf of *Opuntia ficus-indica*. Palisade tissue extends all around. (Figures not drawn to scale.)

DISCUSSION

In previous papers of this series, I have emphasized that the Cactaceae provide unusually comprehensive evidence in the study of highly divergent trends of morphological specializations. These are so bizarre and so closely correlated from ecological and physiological points of view with adaptations for survival in excessively arid environments as to leave few uncertainties regarding the major directions in which phylogenetic changes are progressing.

The most primitive surviving representatives of the Cactaceae from both reproductive and vegetative points of view are considered to occur in the genus *Pereskia*. Such better known species as *P. sacharosa* Griseb. (1962), *P. grandifolia* Haw. and *P. bleo* DC. (1963c), with their large, thin leaves have long been recognized by taxonomists as having a habit of growth and absence of conspicuous succulence characteristic of many typically woody dicotyledonous trees and large shrubs. The leaves of these species have dominantly pinnate vasculature, and photosynthetic activity is largely confined to them. In contrast to this, the relatively thick leaves of *Pereskiopsis* and *Quiabentia* (1960) have prevailingly pseudo-palmate and palmate vasculature. Photosynthetic activity occurs both in leaves and in green parts of succulent elongating shoots (1964a).

Incipient stages of transition from pinnate to pseudo-palmate venation occur in some of the morphologically more specialized species of *Pereskia*, particularly in *P. pititache* Karw. and allied taxa (1960). Summations of evidence from leaves and cotyledons demonstrate that the transitions in vasculature of the Cactaceae are from pinnate to palmate, rather than *vice versa* (1965). Furthermore, incipient modifications of that dense, strongly lignified secondary xylem of such primitive pereskias as *P. sacharosa* and *P. grandifolia* (1963c) occur in various morphologically more specialized species (1962, 1963a, 1963b, 1963d).

However, *Pereskiopsis* and *Quiabentia* differ significantly from *Pereskia* in the absence of sclereids in their secondary phloem (1961a) and in the structure of the outer tissues of their succulent stems. In young green stems of *Pereskiopsis* and *Quiabentia*, there is a precocious development of a crystalliferous hypodermis which is subtended by compact collenchymatous layers and in turn by thin-walled chlorenchymatous tissue (1961b and 1964b). The form of the druses in the hypodermal layer is consistently and characteristically compact and rotund, rather than stellate as in the druses of softer tissues in internal parts of the stems. It is of interest in this connection from functional physiological points of view that there are no intercellular spaces in the apparently impervious collenchymatous layers, the only means of gaseous communication between stomata and intercellular spaces in the chlorenchyma being through special channels in the collenchyma which are jacketed by thick unpitted walls and which tend to have a tenuous inner lining of cutin.

Although a crystalliferous hypodermis is absent in pereskias, and a

structurally homologous form of hypodermis does not occur in the Cereoideae, it develops in characteristic diagnostic form in *Opuntia* and related genera of the Opuntioideae, being present in representatives having flattened green stems, e.g. *O. ficus-indica*, as well as those with cylindrical green shoots, e.g. *O. cylindrica*. It provides significant evidence of relatively close genetic relationships and supports taxonomists (Backeberg, 1966) who include the broad-leaved genera *Pereskia* and *Quiabentia* in the subfamily Opuntioideae. It strengthens my conclusion that the vasculature of terete leaves in this subfamily develops by modifications of palmately veined appendages.

At present the taxonomic affinities of *Maihuenia* with its terete leaves are obscure and uncertain. To place this genus with its highly specialized stems and xylem in the primitive subfamily Pereskioideae (Backeberg, 1966) appears to be premature and discordant. To include it in the Opuntioideae merely on the basis of its terete leaves would be equally unreliable. Similarities in the vasculature of these terete leaves may be due to parallel or convergent evolution rather than indicative of close genetic relationship. Similarities in its pollen and in the highly modified structure of its secondary xylem are suggestive of possible relationship to the Cereoideae, but other morphological features of the genus raise doubts about such a relationship. It is evident that summations of evidence from all organs of the plant and from all species of the genus must be obtained and harmonized in order to determine, if possible, its taxonomic relationships.

LITERATURE CITED

- BACKEBERG, C. 1966. Das Kakteenlexikon. Gustav Fischer. Stuttgart. Classification Paper 17-53.
- BAILEY, I. W. 1960. Comparative anatomy of the leaf-bearing Cactaceae. I. Foliar vasculature of *Pereskia*, *Pereskiaopsis* and *Quiabentia*. Jour. Arnold Arb. 41: 341-356.
- . 1961a. II. Structure and distribution of sclerenchyma in the phloem of *Pereskia*, *Pereskiaopsis* and *Quiabentia*. Ibid. 42: 144-156.
- . 1961b. III. Form and distribution of crystals in *Pereskia*, *Pereskiaopsis* and *Quiabentia*. Ibid. 334-346.
- . 1962. VI. The xylem of *Pereskia sacharosa* and *Pereskia aculeata*. Ibid. 43: 376-388.
- . 1963a. VII. The xylem of pereskias from Peru and Bolivia. Ibid. 44: 127-137.
- . 1963b. VIII. The xylem of pereskias from southern Mexico and Central America. Ibid. 211-221.
- . 1963c. IX. The xylem of *Pereskia grandifolia* and *Pereskia bleo*. Ibid. 222-231.
- . 1963d. X. The xylem of *Pereskia colombiana*, *Pereskia guamacho*, *Pereskia cubensis*, and *Pereskia portulacifolia*. Ibid. 390-401.
- . 1964a. XI. The xylem of *Pereskiaopsis* and *Quiabentia*. Ibid. 45: 140-157.

- . 1964b. XII. Preliminary observations upon the structure of the epidermis, stomata, and cuticle. *Ibid.* 374–389.
- . 1965. XIV. Preliminary observations on the vasculature of cotyledons. *Ibid.* 46: 445–452.
- BOKE, N. H. 1944. Histogenesis of the leaf and areole in *Opuntia cylindrica*. *Am. Jour. Bot.* 31: 299–316.